UNIVERSIDADE FEDERAL DE SANTA MARIA
CENTRO DE CIÊNCIAS NATURAIS E EXATAS
PROGRAMA DE PÓS-GRADUAÇÃO EM BIODIVERSIDADE ANIMAL

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PADRÕES GLOBAIS E PREDITORES DA DIVERSIDADE BETA TAXONÔMICA E FUNCIONAL EM ASSEMBLEIAS DE PEIXES RECIFAIS

Santa Maria, RS
2020

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Dissertação apresentada ao Curso de Pós-Graduação em Biodiversidade Animal, da Universidade Federal de Santa Maria (UFSM, RS), como requisito parcial para obtenção do título de **Mestre em Ciências Biológicas – Área Biodiversidade Animal**.

Orientadora: Profª. Dra. Mariana Bender Gomes

Santa Maria, RS

2020

Maxwell, Melina Forgiarini
PADRÕES GLOBAIS E PREDITORES DA DIVERSIDADE BETA TAXONÔMICA E FUNCIONAL EM ASSEMBLEIAS DE PEIXES RECIFAIS / Melina Forgiarini Maxwell.- 2020.
53 p.; 30 cm

Orientadora: Mariana Bender Gomes
Dissertação (mestrado) - Universidade Federal de Santa Maria, Centro de Ciências Naturais e Exatas, Programa de Pós-Graduação em Biodiversidade Animal, RS, 2020

1. Diversidade beta 2. Turnover 3. Peixes recifais 4. Regiões biogeográficas 5. Riqueza de corais I. Gomes, Mariana Bender II. Título.

Sistema de geração automática de ficha catalográfica da UFSM. Dados fornecidos pelo autor(a). Sob supervisão da Direção da Divisão de Processos Técnicos da Biblioteca Central. Bibliotecária responsável Paula Schoenfeldt Patta CRB 10/1728.

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Aprovado em 11 de março de 2020:

Mariana Bender Gomes

Mariana Bender Gomes, Dra. (UFSM)
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Cristian de Sales Dambros, Dr. (UFSM)

Murilo S Dias

Murilo Sversut Dias, Dr. (UnB) – Videoconferência

Santa Maria, RS
2020

AGRADECIMENTOS

À Universidade Federal de Santa Maria (UFSM) pelo espaço concedido para a realização da minha Pós-Graduação. E, também, aproveito para demonstrar meu orgulho pela UFSM, pois está entre as 10 universidades do mundo com maior produção científica realizada por mulheres.

Ao Programa de Pós-Graduação em Biodiversidade Animal. Agradeço todos os professores, colegas e servidores que contribuíram para minha formação durante esse período.

À Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) pela concessão da bolsa de mestrado.

Aos pesquisadores do Grupo *General Approach to Species Abundance Relationships* (GASPAR), pela compilação e disponibilização do conjunto de dados utilizados em minha dissertação.

Sou imensamente grata a minha orientadora, Drª. Mariana Bender Gomes, por ter me acolhido no Laboratório de Macroecologia e Conservação Marinha. Pela sua assistência, confiança e amizade. Além disso, agradeço por ter me apresentado o mundo dos peixes recifais!

Agradeço aos membros avaliadores da banca, Dr. Cristian Dambros e Dr. Murilo Dias, por terem aceitado o convite e pelas sugestões.

Agradeço ao Dr. Sergio Floeter, Dr. Fabien Leprieur e Dr. Juan Quimbayo pelas sugestões e por aceitarem a co-autoria no artigo.

Aos meus colegas e amigos do Laboratório de Macroecologia e Conservação Marinha e do Laboratório de Ecologia Teórica e Aplicada: Anderson, Bruna, Elisa, Gabriella, Jéssica, Maria Luiza, Prianka, Rafaella, Renato, Samanta e Vitor Hugo. Agradeço o convívio, conversas e cafés!

Aos meus amigos e colegas de profissão: Carine, Felipe, Gabriela, Isadora, Luiza, Mariana e Thaís. Pelo convívio (quase que) diário, conversas, almoços no RU, viagens e parceria de sempre! Vocês são muito importantes para mim!

Aos meus familiares, especialmente aos meus pais Maria Medianeira e Raul. Sou eternamente grata por todo o apoio, esforço e incentivo! Dedico essa conquista a vocês!

RESUMO

PADRÕES GLOBAIS E PREDITORES DA DIVERSIDADE BETA TAXONÔMICA E FUNCIONAL EM ASSEMBLEIAS DE PEIXES RECIFAIS

AUTORA: Melina Forgiarini Maxwell

ORIENTADORA: Mariana Bender Gomes

Um dos principais focos dos estudos macroecológicos é entender a variação espacial da diversidade de espécies e, além disso, avaliar quais são os preditores que a moldam ao longo dos ecossistemas terrestres, dulcícolas e marinhos. A diversidade pode ser mensurada tanto pelo seu valor taxonômico, quanto pelo seu valor funcional. Essa diversidade pode ser particionada em diversidades alfa, beta e gama. A diversidade beta corresponde a diferença na composição de espécies ou atributos funcionais entre pares de comunidades e pode ser dividida em *turnover* ou *nestedness* (aninhamento). O *turnover* corresponde à substituição de espécies/atributos funcionais entre áreas, sendo este padrão relacionado a dispersão de espécies. A biodiversidade marinha também pode ser mensurada através das variações nas espécies e funções que desempenham. Um dos principais centros de diversidade marinha são os ambientes recifais, onde encontram-se os peixes recifais. Os peixes recifais correspondem a mais de 6.000 espécies com ampla distribuição ao longo dos oceanos onde desempenham inúmeras funções essenciais para a manutenção do ecossistema recifal. Os valores de dissimilaridade entre comunidades de peixes recifais tropicais vem sendo utilizados para delimitar regiões biogeográficas e, também, avaliar diferenças (i.e., diversidade beta) nas composições taxonômica, funcional e filogenética. Todavia, ainda não foram conduzidos estudos que avaliam as diferenças na composição de espécies e funções em ampla escala. Dessa forma, os objetivos principais desta dissertação são: (i) avaliar os padrões de diversidade beta taxonômica e funcional de assembleias de peixes recifais em escala global; (ii) investigar a congruência entre diversidade beta taxonômica e funcional entre pares de assembleias de peixes recifais; e (iii) determinar a importância relativa dos preditores ambientais nos padrões de diversidade beta taxonômica e funcional. Além disso, é essencial saber se as mesmas variáveis preditoras influenciam os padrões de diversidade beta taxonômica e funcional em diferentes *realms* marinhos e regiões biogeográficas.

Palavras-chave: Recifes tropicais. Diversidade Beta. *Turnover*. Regiões biogeográficas. *Realms* marinhos.

ABSTRACT

GLOBAL PATTERNS AND DRIVERS OF TAXONOMIC AND FUNCTIONAL BETA DIVERSITY IN REEF FISH ASSEMBLAGES

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One of the main focuses of macroecological studies is to understand the spatial variation and, in addition, to evaluate which are the predictors that shape this variation among terrestrial, freshwater and marine ecosystems. Diversity can be measured by its taxonomic and functional value. Also, this diversity can be partitioned into alpha, beta and gama. Beta diversity corresponds to the difference of species composition or functional traits between pairs of communities e can be divided in turnover and nestedness components. Turnover is the substitution of species/functional traits between areas, being associated with species dispersal. Marine biodiversity can also be measured through variations of species and functions, that them perform. Reef areas are one of the main marine biodiversity centers in the world and have a high diversity of marine organisms, among them the reef fish. Reef fish corresponds to more than 6.000 species with a wide distribution throughout the oceans and it performs essential functions for the maintenance of reef ecosystems. The dissimilarity values between communities of tropical reef fish have been used to delimit biogeographic regions and to evaluate differences (i.e., beta diversity) in taxonomic, functional and phylogenetic compositions. Moreover, there is studies relating beta-diversity patterns to environmental variables at local and regional scales. Thus, the main aims of this dissertation are: (i) to investigate taxonomic and functional beta diversity patterns of reef fish assemblages on a global scale; (ii) to evaluate the congruence between taxonomic and functional and taxonomic beta diversity between pairs of reef fish assemblages; and (iii) to determine the relative importance of environmental predictors in patterns of taxonomic and functional beta diversity. Moreover, it is essential to know if the same predictor variables shape beta taxonomic and functional diversity in different realms and biogeographic regions.

Keywords: Tropical reefs. Beta diversity. Turnover. Biogeographic regions. Marine realms.

SUMÁRIO

INTRODUÇÃO GERAL

Entender a variação espacial na diversidade de espécies e suas forças estruturantes têm sido um dos principais focos em estudos ecológicos e biogeográficos. Estima-se que existam mais de 8.7 milhões de espécies distribuídas ao longo do globo, sendo destas 2.2 milhões exclusivas do ambiente marinho (MORA et al., 2011). Essa diversidade de espécies pode ser traduzida em riqueza de espécies e uniformidade (SIMPSON, 1949). A riqueza de espécies corresponde ao número de espécies observada em determinada área (MAGURRAN, 2013). A partir da riqueza de espécies, WHITTAKER (1960) propôs a divisão da diversidade em três componentes: alfa (α), beta (β) e gama (γ). A diversidade alfa corresponde à riqueza de espécies em uma escala local; a diversidade gama é definida pelo número total de espécies observadas num conjunto regional de locais estudados; e, por fim, a diversidade beta corresponde às alterações na composição de espécies entre dois ou mais locais em uma determinada região (BASELGA, 2010; MAGURRAN, 2013).

Diversas hipóteses buscam explicar quais são os processos responsáveis pelos padrões de diversidade observados na natureza, especialmente aqueles relacionados com as mudanças na composição de espécies (BOWEN et al., 2013; BROWN, 2014). Essas hipóteses envolvem desde processos histórico-evolutivos, que atuam em amplas escalas, até fatores ambientais. Um dos principais padrões observados na estruturação das comunidades, tanto no ambiente terrestre quanto marinho, é o gradiente latitudinal de diversidade. Em suma, esse gradiente prediz um aumento no número de espécies em latitudes menores (i.e., região tropical) e uma diminuição da diversidade em direção a maiores latitudes (WILLIG, KAUFMAN & STEVENS, 2003). O gradiente latitudinal de diversidade é observado em diversos grupos taxonômicos, como mamíferos (KAUFMAN, 1995), aves (BLACKBURN & GASTON, 1996), peixes marinhos (STEVENS, 1996), moluscos (CRAME, 2000), corais (HARRIOT & BANKS, 2002) e plantas (QIAN, 1998). Além da diversidade alfa, o gradiente latitudinal de diversidade tem sido explorado recentemente em um contexto de variação na composição de espécies (i.e., diversidade beta), como registrado em mamíferos (QIAN, BADGLEY & FOX, 2009), plantas vasculares (QIAN & RICKLEFS, 2007), anfíbios (BASELGA, GÓMEZ-RODRÍGUEZ & LOBO, 2012) e invertebrados (BASELGA, 2010).

A diversidade beta corresponde ao grau em que duas ou mais comunidades são dissimilares entre si em relação a composição de espécies e essa característica faz dela uma das principais abordagens utilizadas em estudos ecológicos. Essa métrica de diversidade pode refletir em dois fenômenos distintos, resultantes de processos antagônicos (BASELGA, 2010). BASELGA (2010) particionou a diversidade beta em dois componentes distintos: o *turnover* (substituição) e o *nestedness* (aninhamento). O *turnover* corresponde à substituição de espécies entre áreas, enquanto o *nestedness* ocorre em locais que apresentam um menor número de espécies e são subconjuntos de comunidades taxonomicamente mais ricas (BASELGA, 2010). A limitação de nicho e dispersão de espécies encontram-se relacionadas aos padrões de *turnover* (GASTON, EVANS & LENNON, 2007). Já o componente *nestedness* reflete um processo de perda de espécies, como consequência da extinção seletiva e da colonização de novas espécies (COOK & QUINN, 1995). Portanto, a diferenciação entre os dois componentes da diversidade beta é importante para auxiliar no entendimento de questões biogeográficas, ecológicas e de conservação (BASELGA, 2010).

Os padrões de diversidade beta também podem ser investigados através de uma abordagem funcional. Sob a abordagem beta funcional são mensuradas as variações nos atributos funcionais de espécies entre comunidades (RICOTTA & BURRASCANO, 2008). Os atributos funcionais são características morfológicas, fisiológicas ou fenológicas que influenciam diretamente a performance dos organismos (VIOLLE et al., 2007; MOUILLOT et al., 2013). Estes atributos podem ser utilizados para reunir espécies em entidades ou grupos funcionais (e.g. herbívoros de tamanho médio). Espécies que compõem um grupo funcional têm papeis semelhantes nas comunidades e respondem de forma similar a diferentes variáveis ambientais (LAVOREL et al., 1997). Dessa forma, os grupos funcionais estão relacionados aos processos ecossistêmicos e, também, à resposta de espécies às alterações ambientais (NYSTRÖM, FOLKE & MOBERG, 2000; LUCK, CARTER & SMALLBONE, 2013). Portanto, a abordagem funcional permite compreender a relação entre biodiversidade e funções ecossistêmicas, oferecendo informações complementares à riqueza e diversidade taxonômica (CADOTTE, CARSCADDEN & MIROTCHNICK, 2011; LAURETO, CIANCIARUSO & SAMIA, 2015).

A biodiversidade marinha pode ser avaliada através da variação das espécies e, também, das funções realizadas no ecossistema marinho. Para vertebrados e invertebrados marinhos são observados distintos padrões de diversidade: as espécies costeiras apresentam máxima diversidade no Pacífico Ocidental, enquanto as espécies oceânicas mostraram picos de diversidade em latitudes de 30º norte e sul (TITTENSOR et al., 2010). Um dos principais centros de biodiversidade no ambiente marinho são as áreas recifais (SALA & KNOWLTON, 2006). Os recifes de corais são comparados a florestas tropicais, devido a sua alta diversidade de espécies e complexidade estrutural (CONNEL, 1978; REAKA-KUDLA, 1997). Nos ecossistemas recifais, dentre os grupos altamente diversos, encontram-se os peixes recifais. Os peixes recifais correspondem a mais de 6,000 espécies distribuídas ao longo dos oceanos Atlântico, Pacífico e Índico (KULBICKI et al., 2013). Além da elevada diversidade taxonômica e ampla distribuição, os peixes recifais desempenham inúmeras funções afetando diretamente a dinâmica dos ambientes recifais (e.g., movimento de energia/matéria) (BELLWOOD & WAINWRIGHT, 2002). Entretanto, algumas funções ecossistêmicas essenciais são desempenhas por poucas espécies de peixes recifais (HUGHES et al., 2017), mostrando que recifes de corais são vulneráveis a perda de espécies funcionalmente importantes (MOUILLOT et al., 2014). Dessa forma, a elevada riqueza de espécies e ampla distribuição de peixes recifais, além da variedade de funções ecossistêmicas desempenhadas pelos mesmos, tornam os peixes recifais um modelo ideal para o estudo na variação da diversidade (i.e., diversidade beta) ao longo dos oceanos e suas regiões biogeográficas.

A partir das diferenças taxonômicas observadas entre ambientes recifais, foram delimitados três reinos (*realms*) marinhos e seis regiões biogeográficas (KULBICKI et al., 2013). Os três reinos marinhos foram denominados Atlântico, Pacífico Oriental Tropical e Indo-Pacífico (KULBICKI et al. 2013). Cada reino marinho apresenta sua história ecológica-evolutiva e barreiras biogeográficas que isolam diferentes comunidades de peixes recifais (FLOETER et al., 2008; KULBICKI et al. 2013; BELLWOOD et al. 2015). Além de utilizar as dissimilaridades entre as comunidades de peixes recifais para delinear regiões biogeográficas, estas têm sido utilizadas para avaliar os padrões de diversidade beta taxonômica e filogenética em escalas locais e regionais (ARIAS-GONZÁLEZ et al., 2008; HATTAB et al., 2015; PINHEIRO et al., 2018; CARLOS-JÚNIOR et al., 2019). No mar Mediterrâneo, a diversidade beta taxonômica de peixes costeiros está principalmente relacionada com profundidade e temperatura da superfície do mar (HATTAB et al., 2015). No Caribe, o componente *turnover* (i.e., substituição de espécies) está relacionado principalmente com a área recifal, mas também com profundidade e cobertura de corais (ARIAS-GONZÁLEZ et al., 2008). No Sudoeste Atlântico, PINHEIRO et al. (2018) observou maiores valores de diversidade beta taxonômica entre o Uruguai e o sul do Brasil, além de dois estados no nordeste brasileiro e, por fim, em ilhas oceânicas. Os principais preditores da composição de assembleias de peixes recifais na província Brasileira foram uso de habitat, tamanho corpóreo, profundidade e dieta (PINHEIRO et al., 2018). Na Baia de Ilha Grande, no sudeste brasileiro, as variações na composição de espécies de peixes recifais está relacionada com as diferenças de profundidade, assim como, em padrões de abundância (CARLOS-JÚNIOR et al., 2019). Estes estudos sobre diversidade beta em comunidades de peixes recifais, geralmente, são conduzidos em escalas menores e relacionam os padrões encontrados apenas com variáveis ambientais.

Apesar dos padrões de diversidade alfa e gama, bem como a história evolutiva de peixes recifais terem sido estudados em ampla escala geográfica, as diferenças (i.e., diversidade beta) na composição taxonômica e funcional de assembleias de peixes recifais ainda não foram conduzidas em ampla escala. Além disso, pouco se sabe sobre a influência de variáveis ambientais e geográficas na formação e manutenção dos padrões de diversidade beta funcional e taxonômica em assembleias de peixes recifais em distintos reinos marinhos e regiões biogeográficas. Dessa forma, os principais objetivos deste estudo são: (i) investigar os padrões de diversidade-β taxonômica e funcional em escala global, (ii) investigar a congruência entre padrões de diversidade-β taxonômica com os padrões de diversidade-β funcional entre assembleias de peixes recifais; e, por fim, (ii) identificar os fatores ambientais que contribuíram para moldar as variações na diversidade-β taxonômica e funcional em diferentes regiões biogeográficas.

Estrutura da dissertação

Esta dissertação é apresentada em um capítulo único, estruturado em formato de “*Original research”*, conforme as normas da revista *Ecography*.

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Global patterns and drivers of taxonomic and functional beta diversity in reef fish assemblages

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Abstract

Beta diversity corresponds to differences in species composition and/or functional traits between sites. Reef fishes are the most diverse group of marine vertebrates, corresponding to more than 6.000 species and being widely distributed across the oceans. Also, they develop several and essential functional roles for the maintenance of reef ecosystems. Here, we investigated the patterns of taxonomic and functional beta diversity contrasting pairs of reef fish assemblages in the Atlantic, Tropical Eastern Pacific and Indo-Pacific realms. In the Atlantic, a clear taxonomic and functional dissimilarity between reef fish faunas from the Caribbean and the Southwestern Atlantic were structured by coral richness. Fish assemblages of Tropical Eastern Pacific were shaped by their distance from the biodiversity center in the Indo-Australian Archipelago, and a functional split between north, south and oceanic islands possibly reflects thermal gradients along this realm. The Indo-Pacific realm showed highly homogeneous taxonomic and functional beta diversity values. Distance from the Quaternary reef refugia had a key role in shaping the beta diversity of this realm. Correlations between functional and taxonomic beta diversity as well as between its turnover components reveals that differences in species composition are followed by differences in the functional structure of fish assemblages.

Keywords: Tropical reefs. Beta diversity. Turnover. Biogeographical boundaries. Isolation.

1. Introduction

Understanding the patterns and processes that shape biodiversity, as well as their variations throughout space and time, have been in the center of macroecology (Harborne et al. 2006, Siqueira et al. 2016, Lyons et al. 2019, Pontarp et al. 2019). In an attempt to unrevealing these patterns, several metrics have been incorporated into studies of biological communities, such as taxonomic, functional and phylogenetic diversities (Meynard et al. 2011, Strecker et al. 2011, Swenson 2011, Arnan et al. 2017, Teichert et al. 2018). Differences in the taxonomic, functional and phylogenetic composition are associated with environmental heterogeneity (Price 2002, Veech and Crist 2007, Arias-González et al. 2008, Melo et al. 2009, Bozelli et al. 2015, López-Delgado et al. 2015) and spatio-temporal scales (Carstensen et al. 2014, Fordyce and DeVries 2016, Rocha et al. 2018, Legendre 2019). Environmental heterogeneity, for instance, promotes the increase of species richness of birds (Veech and Crist 2007), plants (Dufour et al. 2006), corals and reef fish (Ariaz-González et al. 2008). While different spatio-temporal scales influence species richness within and between communities (Willis and Whittaker 2002). Clarke and Lidgard (2001) examined Bryozoan’s assemblages in the North Atlantic and observed that on a local scale there was no variation in species composition with latitude, however, on a regional scale there was a peak in species richness among tropical and temperate areas.

Species diversity is commonly divided into three levels: alpha, beta and gamma (Whittaker 1960). Alpha diversity (α) consists in the number of species in a unique site or habitat; gamma diversity (γ) is measured by the species richness in a region and, finally, the beta diversity (β) represents the differences in species composition between two or more habitats into a region (Mittelbach 2012). Beta diversity interacts with local diversity (i.e., alfa diversity) and both result from community assembly through local and regional filters (Soininen et al. 2018). Beta diversity can be partitioned into two components: (i) turnover, which represents the replacement of species or functions between assemblages; and (ii) nestedness, where assemblages with lower species richness or functional richness are subsets of assemblages with higher species richness (Baselga 2010, Villéger et al. 2013). In biological communities, the turnover component can be related to dispersion processes, while nestedness can be related to selective colonization and extinction (Si et al. 2016). The assessment of beta diversity components may support the understanding of biogeographic, ecological and conservation issues (Baselga 2010).

Taxonomic diversity often corresponds to species richness and these species are functionally different from each other (Villéger et al. 2013). However, an approach focused only in species identity is limited relative to the understanding of community assembly, as well as the diversity effects on ecosystem functioning (Villéger et al. 2008, Mouillot et al. 2011). Functional diversity is based on life-history traits of each specie, which are defined as characteristics that influence growth and survival aspects of organisms (Violle et al. 2007). Traditionally, under a functional approach, species are grouped by their functional, morphological and/or physiological traits into functional entities (Wright et al. 2006). Functional entities provide information about the structure and dynamics of assemblages and depending on functional redundancy, the addition or loss of species may have impacts on ecosystem functioning (Halpern and Floeter 2008, Estes et al. 2016, Denis et al. 2017, Heilpern et al. 2018). Once species interact locally through their attributes, approaches that include the functional component of communities may be utilized to understand ecosystem functioning and services (Lavorel et al. 2011, Cadotte 2017, Winfree et al. 2018), functional diversity patterns (Cadotte et al. 2011, Meynard et al. 2011, Pimiento et al. 2017), and assemblage's responses to environmental changes (Mayfield et al. 2005, Mouillot et al. 2013). Thus, both taxonomic and functional diversity have been widely used in studies that assess the difference in composition between two or more communities (Devictor et al. 2010, Villéger et al. 2012, Leão-Pires et al. 2018, Carvalho et al. 2019)

Studies investigating taxonomic and functional beta-diversity patterns have already been conducted in terrestrial ecosystems from local to global scale (Qian & Ricklefs 2007, Melo et al. 2009, Qian 2009, Baselga et al. 2012, Fluck et al. 2020). In the Amazonian forest, taxonomic and phylogenetic turnover of passerine birds is mainly driven by temperature and geographic distance (Fluck et al. 2020). At global scale, differences in amphibian diversity are explained by higher turnover values in the tropical region, whereas higher nestedness values characterize assemblages at higher latitudes (Baselga et al. 2012). For mammals and birds, beta diversity patterns have been shown to be related to habitat heterogeneity and current climatic conditions (Melo et al. 2009). However, studies of taxonomic and functional beta diversity in marine ecosystems are generally conducted at a local or regional scale (Becking et al. 2006, Carlos-Júnior et al. 2019). As observed in terrestrial environments, the variation in species composition and/or functions between locations is frequently associated with the high heterogeneity found in marine ecosystems for starfishes, corals and reef fishes (Price 2002, Arias-González et al. 2008). Yet there are no global scale assessments of beta diversity patterns for marine communities using a functional approach.

Reef ecosystems harbor remarkable species diversity and ecosystem functions. There are over 6.000 fish species inhabiting reefs distributed across the world's oceans (Kulbicki et al. 2013). The marine biodiversity hotspot in the Indo-Australian Archipelago – the Coral Triangle – hosts more than 2.000 reef fish species (Pellissier et al. 2014). As the distance from the Coral Triangle increases, reef fish richness decreases (Bellwood et al. 2012, Mouillot et al. 2013, Parravicini et al. 2013). Also, this marine biodiversity hotspot played several roles in structuring reef fish communities and acted as a center of origin, overlap, accumulation and survival of species (Bellwood et al. 2012, Bowen et al. 2013, Bellwood et al. 2015). In the Atlantic Ocean, the biodiversity center is located in the Caribbean, where more than 800 reef fish species are found and about ¼ of these being endemic (Floeter et al. 2008). This high taxonomic diversity translates into countless functions performed by fishes in reef ecosystems (Mouillot et al. 2014, Villéger et al. 2017). Even though the reef fish assemblages are taxonomically diverse, several species can be highly functionally redundant (i.e., over-redundant), and others are functionally vulnerable (i.e., particular functions are performed by a single species) (Mouillot et al. 2014). As isolation from the Indo-Australian Archipelago and from surrounding reef areas increases, the functional structure of reef fish communities is nested in within the functional structure of richer sites (Bender et al. 2017). However, differences in taxonomic and functional compositions between communities are poorly known. Thus, the species richness and diversity of functions, as well as the wide distribution patterns, makes reef fish a model group in beta diversity studies.

Tropical reef fish assemblages are grouped into three biogeographic realms, namely the Atlantic, the Tropical Eastern Pacific and the Indo-Pacific, as well as six biogeographic regions, based on dissimilarity of species composition (Kulbicki et al. 2013). Each marine realm has a different evolutionary history (Bellwood et al. 2002, Bellwood and Wainwright 2002, Floeter et al. 2008, Robertson and Craemer 2008). While the Tropical Eastern Pacific and the Atlantic realms have a history of isolation, due to the presence of biogeographical barriers, the Indo-Pacific has been more connected through time, acting both as a refuge for lineages as exporting reef fish diversity to other realms and regions (Bowen et al. 2013, Pellissier et al. 2014, Bellwood et al. 2015). At these scales is possible to relate variations in taxonomic and functional diversity with the presence of biogeographic barriers, changes in sea-level, plate tectonics movement, as well as dispersion, colonization and environmental filters (Renema et al. 2008, Bellwood et al. 2012, Bellwood et al. 2015). The Indo-Pacific realm has a higher dissimilarity in reef fish species composition within its regions, which supports processes of dispersion and colonization at broader scales (Kulbicki et al. 2013). On a broad spatio-temporal scale, environmental predictors may be important to shape diversity patterns as well as differences in assemblage structure and composition (Parravicini et al. 2013, Pellisier et al. 2014, Bender et al. 2017, Barneche et al. 2019). On a regional scale, Bellwood and Hughes (2001) observed that shallow-water habitat availability and longitude were the major predictors of variation in the taxonomic composition of reef fish in the Indo-Pacific realm. While in the Atlantic and the Tropical Eastern Pacific realms a higher dissimilarity of reef fish species as well levels of endemism are observed, which may be associated with the presence of biogeographical barriers between regions (Kulbicki et al. 2013). Historical-evolutionary processes have contributed to shaping the diversity of life at large scales (Ricklefs 2004). Therefore, relating environmental variables to taxonomic and functional diversity patterns may explain differences in the composition of reef fish assemblages across marine realms and its regions. Furthermore, it is unknown the extent to which environmental predictors shape the patterns of taxonomic and functional beta diversity in reef fish assemblages at a global scale. Thus, in this study, our main aims were: (i) to evaluate taxonomic and functional beta diversity patterns of reef fish assemblages on a global scale, (ii) to investigate the congruence between taxonomic and functional beta diversity between pairs of reef fish assemblages; and (iii) to determine the relative contribution of environmental and historical predictors in patterns of taxonomic and functional beta diversity.

2. Material and Methods

2.1. *Reef fish database*

The database was compiled by the GASPAR (General Approach to Species-Abundance Relationships) research group (Kulbicki et al. 2013, Parravicini et al. 2013, Mouillot et al. 2014, Bender et al. 2017). The reef fish presence/absence data were compiled from published works, checklists, monographs and scientific reports (Parravicini et al. 2013). This data covers 6254 reef fish species distributed in three marine realms (*sensu* Kulbicki et al. 2013): the Atlantic, Tropical Eastern Pacific and Indo-Pacific (Figure 1-A). Also, the Indo-Pacific realm was divided into three biogeographic regions: Central Indo-Pacific, Central-Pacific and Western Indian (*sensu* Kulbicki et al. 2013) (Figure 1-B). The Indo-Pacific realm was divided into its biogeographical regions due to its vast extent and the high similarity between assemblages, from east to west, over large biogeographical scale (Kulbicki et al. 2013).The marine realms and biogeographic regions were divided into grid cells of 5º by 5º degrees (~550 km at the Equator), totalizing 303 cells. This grid size was used previously in reef fish studies (Parravicini et al. 2014, Pelissier et al. 2014) and is considered appropriate given the resolution and available geographic information for the reef fish fauna.

2.2. *Traits and functional entities*

The reef fish species were classified into six categorical traits: 1) Maximum body size (0-7 cm, 7.1-15 cm, 15.1-30 cm, 30.1-50 cm, 50.1-80 cm and >80 cm); 2) Trophic categories (herbivorous-detritivorous, planktivorous, piscivorous, omnivorous, macroalgal herbivorous, invertivorous targeting sessile invertebrates and invertivorous targeting mobile invertebrates); 3) Mobility (sedentary – including territorial species –, mobile between reefs and mobile within a reef); 4) Period of activity (diurnal, nocturnal or both); 5) Schooling (solitary, pairing, small groups – 3-20 individuals –, medium groups – 20-50 individuals –, and large groups – >50 individuals –; and 6) Vertical position in the water column (pelagic, benthopelagic and benthic). Functional entities were defined as a combination of these six categorical functional traits. Traits were also available from the GASPAR database (Bellwood et al. 2004, Ferreira et al. 2004, Halpern and Floeter 2008, Mouillot et al. 2014, Parravicini et al. 2014, Bender et al. 2017).

2.3. *Environmental data*

In GASPAR database, sets of environmental predictors associated with each grid cell are available. From GASPAR database, we selected seven environmental predictors and measured its influence on patterns of reef fish beta diversity: current reef area (km^2), isolation from the nearest reef areas (km), distance from biodiversity center (km) – the Indo-Australian Archipelago (IAA) in the Indo-Pacific realm and the Caribbean in the Atlantic realm –, distance from the Quaternary refugia (km), coral richness, mean sea surface temperature (SST), and mean chlorophyll-a. The current reef area and coral richness were estimated from the Coral Reef Millennium Census Project (Andrefouet et al. 2006). The isolation from de nearest reef areas was obtained based on the connectivity between each site to the 10 nearest reef habitats (Parravicini et al. 2013). The distance from the biodiversity center was measured for each marine realm, considering the Caribbean for sites in the Atlantic realm and the Indo-Australian Archipelago for sites within the Indo-Pacific realm. These predictors – isolation from the nearest reef areas and distance from the biodiversity center – have been used as a proxy for connectivity (Parravicini et al. 2013, Pellissier et al. 2016, Bender et al. 2017). The distance from the Quaternary reef refugia was estimated as the mean past reef area for the period which the sea surface temperature was lower than the 10th percentile of all periods. Also, the mean sea surface temperature and mean chlorophyll-a were extracted for each cell with a spatial resolution of 5 arcmins from Bio-ORACLE (Tyberghein et al. 2012, Assis et al. 2018).

To eliminate collinearity between environmental predictors we performed Pearson's correlations between all pairs of variables at the realm and biogeographic region scales. When correlation coefficients were ≥ 0.7, one of the variables were excluded considering its biological relevance for reef fish assemblages (Figure S1). Resultant variables for each marine realm and Indo-Pacific biogeographic regions are in the Supplementary material (Table S1). These variables have been widely used in global scale studies of reef fish diversity (Bellwood et al. 2005, Parravicini et al. 2014, Bender et al. 2017, Barneche et al. 2019).

2.4. *Data analysis*

We have assessed beta-diversity patterns at the 5°x5° grid cell scale for the Atlantic, the Tropical Eastern Pacific, the Indo-Pacific realms, and for the Central Indo Pacific, Central Pacific and Western Indian biogeographic regions of the Indo Pacific realm (Kulbicki et al. 2013). Taxonomic beta-diversity was measured as the dissimilarity between pairs of reef fish assemblages using the Sorensen's index (Tß$_{sor}$) and the turnover component (Tß$_{sim}$) (i.e., species substitution without the influence of richness gradients) (Baselga 2010, Baselga 2012). The Sorensen's dissimilarity index is expressed as the following formula

$$\mathbf{sor} = \frac{\boldsymbol{b} + \boldsymbol{c}}{\boldsymbol{2a} + \boldsymbol{b} + \boldsymbol{c}}$$

and the turnover component of the Sorensen's dissimilarity index is expressed by

$$\mathbf{sim} = \frac{\boldsymbol{min}\,(\boldsymbol{b},\ \boldsymbol{c})}{\boldsymbol{a} + \boldsymbol{min}\,(\boldsymbol{b},\ \boldsymbol{c})}$$

Where *b* is the number of species that are found exclusively in the first site, *c* is the number of species exclusive to the second site and *a* is the number of species common to both sites. We also calculated the functional beta diversity among pairs of reef fish assemblages. We first computed functional dissimilarity matrices applying the Gower’s distance to sets of species traits observed in each marine realm and biogeographic region. A Principal Coordinate Analysis (PCoA) was performed in each of these dissimilarity matrices. Functional beta diversity was also calculated through the Sorensen’s index ($Fß_{sor}$) and the turnover component ($Fß_{sim}$).

To test for correlations between the total functional ($Fß_{sor}$) and taxonomic ($Tß_{sor}$) beta diversity, as well as between the functional turnover ($Fß_{sim}$) component and taxonomic turnover component ($Tß_{sim}$), we performed Spearman’s correlations for each marine realm and Indo-Pacific biogeographic region.

2.5. *Ordination*

Ordination methods are commonly used in broad-scale biogeography studies and allow the identification of biogeographical transition zones (Hattab et al. 2015). Moreover, ordination represents a useful and heuristic method to visualize a global assemblage distance matrix and to evaluate the relationships between regions according to their composition (Kreft and Jetz 2010). For each functional and taxonomic dissimilarity matrix obtained, we performed a two-dimensional non-metric multidimensional scaling (NMDS) neighbour-joining algorithm with 20 random starts to find a stable solution (Oksanen et al. 2019). Then, the values of the two NMDS axes were plotted in individual maps with 5°x5° grid cells for each marine realm (Atlantic, Tropical Eastern Pacific and Indo Pacific) and the biogeographic regions of the Indo Pacific (Central Indo Pacific, Central Pacific and Western Indian). Stress values are the sum of squared differences between the fitted and original distances and were used to assess how well the configuration of points in the reduced ordination space matched the original distance matrix (Legendre and Legendre 1998). Stress values lower than 0.05 provide excellent representation in reduced dimensions, < 0.1 is a great ordination, < 0.2 is a good ordination value, and stress values greater than 0.2 provide a poor representation (Clarke 1993).

2.6. *Environmental predictors and taxonomic/functional beta diversity*

To estimate the relative importance of each environmental predictor in the observed patterns of Tßsor, Tßsim, Fßsor and Fßsim in each marine realm and Indo-Pacific biogeographic regions we used the ‘envfit’ function in R package *vegan* (Oksanen et al. 2019). This function fits the environmental predictors onto an ordination and estimates the strength of the correlations between the NMDS ordinations and the selected environmental predictors. Also, the ‘envfit’ function provides an objective interpretation of the results of the ordination analysis and generates a measure of fitted vectors, as well as significant value based on a permutation test with 999 permutations.

All data analyses were performed using the software R 3.6.1 (R Core Team 2019) and the following packages: betapart (Baselga and Orme 2018), cluster (Maechler et al. 2019), vegan (Oksanen et al. 2019), recluster (Dapporto et al. 2015), rgdal (Bivand et al. 2019), shape (Soetaert 2018), GISTools (Brunsdon and Chen 2014), Hmisc (Harrell 2019), corrplot (Wei and Simko 2017). We also used the functions ‘functional.beta.pair5’(available in <https://github.com/csdambros/R-functions/blob/master/FunctionalBetaPart.R>, Dambros, C.) and ‘Map the world’ (Albouy, C. and Leprieur, F.) in the analysis.

3. Results

For the Atlantic and Tropical Eastern Pacific realms, as well as for the Western Indian region, the NMDS ordinations led to satisfactory projections of dissimilarity matrices into two-dimensional space (Table 1), as seen in the relatively low-stress values obtained. High-stress values were observed for the Indo-Pacific realm where taxonomic and functional turnover components corresponded to 0.211 and 0.233, respectively. A high-stress value (0.212) was also observed for the taxonomic turnover of the Central Indo-Pacific region.

The spatial patterns for the total taxonomic and functional beta diversity and turnover component were visualized using color maps, where similar colors in grid cells predicted assemblages with similar taxonomic (species) or functional (traits) composition. Therefore, grid cells with different colors are predicted to have more dissimilar species composition or functional group structure. In the Atlantic realm, the patterns observed for total taxonomic beta diversity and its turnover component were very similar (Figure 2-A), where a clear separation between the Eastern and Western Atlantic reef fish faunas, and from the Brazilian oceanic islands can be visualized. However, the total functional beta diversity values reveal that the Caribbean and the Brazilian coast have similar functional structure (Figure 2-A). Yet there is a clear division between the functional turnover present in the Caribbean and the Brazilian coast. In the Tropical Eastern Pacific realm, total taxonomic and functional beta diversity, as well its turnover components, display different spatial patterns. A latitudinal gradient is observed for taxonomic turnover values, while functional turnover reveals a clear separation between north, south and Tropical Eastern Pacific oceanic islands (Figure 3-A). In the Indo-Pacific realm, total taxonomic and functional beta diversity reveals a spatially homogeneous pattern, yet differences appear in the turnover component (Figure 4-A). The pattern observed for taxonomic beta diversity is a longitudinal (East-West) color gradient, with some exceptions to isolated oceanic islands, as Desventuradas Islands and Easter Island (near to Tropical Eastern Pacific) and reef areas located at higher latitudes (Figure 4-A). At this scale, the taxonomic turnover pattern has revealed the existence of three regions with similar turnover values among pairs of assemblages: the Western Indian, the Central Pacific along with the Central-Indo Pacific, and the Hawaiian Archipelago. While there is homogeneity in total functional beta diversity values for the Indo-Pacific realm, the turnover component reveals there are similar values for reef fish assemblages that inhabit the Indo-Australian Archipelago area, a biodiversity hotspot (Figure 4-A). At the regional scale, the Central Indo-Pacific showed a homogenous pattern of variation in species composition (Figure S2-A), with exceptions in Western Australia. However, taxonomic turnover displays a heterogeneous pattern. Moreover, both functional beta diversity and functional turnover have a homogeneous pattern in the Indo-Australian Archipelago and its nearby regions, but as the distance from this area increases, functional dissimilarity also increases (Figure S2-A). Both total taxonomic and functional beta diversity have similar patterns in the Central Pacific region (Figure S3-A), which may imply that changes in taxonomic composition are followed by changes in functional composition. The Western Indian showed a north-south gradient in total taxonomic beta diversity, with the most dissimilar assemblages located in southern Africa (Figure S4-A).

Overall, practically all environmental variables were significant when correlated with two NMDS axes (Table 2, Tables S2-S3-S4). Great differences were not detected in the influence of environmental predictors in both taxonomic and functional beta diversity as well as turnover component (Tables S3-S4).

For the Atlantic realm, mean sea surface temperature was highly correlated with the first NMDS axis, while mean chlorophyll-a was strongly associated with the second NMDS axis (Table 2). In the Tropical Eastern Pacific realm, the distance from the biodiversity center was strongly associated with the first NMDS axis and isolation from the nearest reef areas was highly associated with the second NMDS axis. For the Indo-Pacific realm, current reef area, isolation from the nearest reef areas and mean sea surface temperature were strongly associated with the first NMDS axis, while mean chlorophyll-a was associated with the second NDMS axis (Table 2). At the regional scale, the Central Indo-Pacific beta-diversity values were influenced by distance from the biodiversity center, mean chlorophyll-a and isolation from the nearest reef area in the second NMDS axis. In the Central Pacific, isolation from Quaternary refugia as well as coral richness has influenced the first NMDS axis, while the distance from the biodiversity center and current reef area were highly correlated with the second NMDS axis. Finally, for the Western Indian, reef area, and distance from Quaternary refugia showed high correlated values with the first NMDS axis, and mean chlorophyll-a and coral richness were strongly associated with the second NMDS axis (Table S2).

Overall, the environmental predictors with the greater relative importance ($R^2 \geq 0.6$) were coral richness, distance from the biodiversity center, distance from Quaternary refugia and isolation from the nearest reef areas (Figures 2-C, 3-C, 4-C). For the Indo-Pacific regions (Central Indo-Pacific, Central Pacific and Western Indian) the environmental predictors with the greater relative importance were distance from Quaternary refugia and coral richness (Figures S1-C, S2-C, S3-C).

Correlations among total taxonomic and functional beta diversity values have revealed that variations in these components are mostly congruent in global reef fish faunas. However, pairwise values for total taxonomic beta diversity are higher than those of total functional beta diversity (e.g., $Tß_{sor}$ varied from 0.0 – 1.0, while $Fß_{sor}$ varied from 0.0 – 0.15 in the Atlantic). Assemblages of the Tropical Eastern Pacific showed the higher correlation value (rho = 0.84; $p < 0.001$) between total functional ($Fß_{sor}$) and total taxonomic ($Tß_{sor}$) beta diversity, followed by the Atlantic (rho = 0.80; $p < 000.1$) and Indo-Pacific (rho = 0.70; $p < 0.001$) realms (Figures 5-A, 5-C, 5-E). The turnover component had lower, yet significant, correlation values (Figures 5-B, 5-D, 5-F). In general, Indo-Pacific biogeographic regions depicted highly correlated total functional ($Fß_{sor}$) and total taxonomic ($Tß_{sor}$) beta diversity (Figures S4-A, S4-C, S4-E). However, the functional ($Fß_{sim}$) and taxonomic ($Tß_{sim}$) turnover component had low correlation values.

4. Discussion

In our study, we mapped taxonomic and functional beta diversity between pairs of reef fish assemblages at a global scale and we observed that patterns differ across biogeographical realms. While taxonomic and functional composition of assemblages are in line with biogeographic regions for the Atlantic, as well as observed in other studies (Floeter et al. 2008, Cowman and Bellwood 2013, Kulbicki et al. 2013). In Tropical Eastern Pacific and the Indo-Pacific realms, differences in taxonomic and functional structure are not related to the boundaries that limit/establish regions, as found in other studies (Cowman and Bellwood 2013, Kulbicki et al. 2013). These differences in beta diversity observed in each marine realm and biogeographic region can be related to the different evolutionary histories or the evolution of reef fish taxonomic and functional groups (Bellwood et al. 2015). On the other hand, we identified that environmental and historical/geographic predictors on taxonomic and functional beta diversity varies according to realms. For instance, coral richness is the most important predictor to the Atlantic realm, distance from the biodiversity center to the Tropical Eastern Pacific and from the Quaternary refugia to the Indo-Pacific realm. These results are in accordance with previous studies, who identified these predictors how the most important drivers that explain reef fish diversity (Parravicini et al. 2013, Pellissier et al. 2016, Bender et al. 2017). We have also found that greater differences in species composition ($Tß_{sor}$) between assemblages are followed by functional differences ($Fß_{sor}$), yet variations in functional beta diversity were smaller than variations in taxonomic beta diversity.

In the Atlantic realm, the Mid-Atlantic Ridge, the freshwater outflow from the Amazon and Orinoco rivers, as well as Benguela barrier act as filters, limiting the dispersion of reef fishes (Floeter et al. 2008, Pinheiro et al. 2018). However, it is possible that some species can occasionally cross these inter-regional barriers and allow colonization of new groups of species (Floeter et al. 2008). More than 60% of species found in the Eastern Atlantic are restricted to this region (Floeter et al. 2008). Despite the presence of the Amazon-Orinoco outflow barrier, which separates the Southwestern Atlantic and Northwestern Atlantic (Caribbean) reef fish assemblages, the observed patterns of total taxonomic beta diversity and taxonomic turnover component were similar (Figure 2-A). These results could be associated with a higher number of shared species and sister’s species between these regions (Floeter et al. 2008). Also, we observed similar patterns of total functional beta diversity between the Southwest Atlantic and the Northwest Atlantic, which can be explained by a similar functional structure – relative to trophic groups – identified for Atlantic Ocean reef fish assemblages (Bender et al. 2013). Total beta diversity patterns identified for the Mid-Atlantic Ridge, Fernando de Noronha Archipelago, Rocas Atoll and Vitória-Trindade Seamount Chain oceanic islands can be related with isolation from the mainland and the distance from the biodiversity center (Floeter et al. 2008, Bender et al. 2013, Quimbayo et al. 2019). Also, the total functional differences for the above-mentioned islands are possibly related to differences in traits. In the Atlantic, as well as in other realms, island reef fish assemblages are characterized by a predominance of traits as large body size and carnivorous diets (Bender et al. 2013, Kulbicki et al. 2015).

In the Tropical Eastern Pacific (TEP), the latitudinal gradient in taxonomic turnover could be related with both historical origins of the realm (Robertson and Cramer 2009) and reef fish range size (Mora and Robertson 2005a, Alzate et al. 2019). For instance, the Gulf of California began to form ~25 Mya, favoring that population in the north of the TEP became isolated and contributing to the development of the distinctive tropical and subtropical fauna. While in the Isthmus of Panama (~3 Mya), several tropical species from the Caribbean were isolated favoring another fish fauna (Robertson and Cramer 2009). On the other hand, this realm has acted mainly as a center of accumulation for reef fish species (Bellwood et al. 2015) as a result of the strong isolation by the Isthmus of Panama, the Gulf of California and the Eastern Pacific barrier (Zapata and Robertson 2006). Few studies have examined diversity patterns of reef fish assemblages in the TEP (Mora and Robertson 2005a, Mora and Robertson 2005b, Robertson and Cramer 2009, Quimbayo et al. 2017). TEP presents high endemism levels, as well as high functional diversity, which is commonly represented by vulnerable reef fish species (Quimbayo et al. 2017). Functional turnover splits north, south and oceanic islands of TEP, which could be related to the thermal gradients along the north-south extension (Hastings 2000). The variation in sea surface temperature may select functional traits, such as body size (Kulbicki et al. 2015) and diet (Floeter et al. 2005), and shape functional turnover among these areas. Oceanic islands, for example, are subsets of mainland coastal species and transpacific residents in the TEP (Robertson et al 2004, Robertson and Cramer 2009), which could imply in the taxonomic and functional dissimilarity observed. Moreover, reef fish communities from northern TEP have a high degree of functional redundancy (Aguilar-Medrano and Calderon-Aguilera 2016), which can be associated with a similar functional beta diversity pattern observed for this region.

The Indo Pacific realm has the main reef fish biodiversity hotspot, named the Indo-Australian Archipelago. In the Miocene (23 – 5 Mya), this biodiversity hotspot was the major source of lineage exportation for the Pacific and Indian Oceans (Bellwood et al. 2015). Moreover, the Indo-Australian Archipelago acted as a center of accumulation, survival and origin of reef fish species (Cowman and Bellwood 2013, Bellwood et al. 2015), being composed primarily by species with large geographic ranges (Connolly et al. 2003). However, during the formation of the Indo-Australian Archipelago, a biodiversity hotspot was already existent in the Western Indian region, the West Tethys (Renema et al. 2008). Over evolutionary time, the Indo-Pacific realm has remained largely connected, especially in the Coral Triangle where shallow-water habitats have been available and connected (Pellissier et al. 2014). This connection explains the similarity in functional and taxonomic beta diversity patterns identified for this realm. Diversity outposts, as Desventuradas Islands and Easter Island have presented dissimilar values, which could be related to high level of endemism, low latitude and distance from the Indo-Australian Archipelago (Allen 2008, Dyer and Westneat 2010, Kulbicki et al. 2013). The total functional similarity observed in the Indo-Pacific realm may be related to the high functional redundancy (over-redundancy) of the reef fish fauna within its biogeographic regions (Mouillot et al. 2014). The functional homogeneity of the Indo-Australian Archipelago (Figures 4 and S2-A) could be related to the contribution of certain traits to the diversity of this region, as small-bodied, planktivorous and diurnal species (Kulbicki et al. 2015, Ottimofiore et al 2017, Floeter et al. 2018).

The main environmental and geographic predictors for total taxonomic and functional beta diversity across all realms are coral richness, distance from the biodiversity center and distance from Quaternary refugia. It is well known that these predictors are important to the structuring of reef fish communities at different spatial scales (Arias-González et al. 2008, Rodríguez-Zaragoza and Arias-González 2008, Bender et al. 2013, Parravicini et al. 2013, Pelissier et al. 2014, Bender et al. 2017, Barneche et al. 2019, Quimbayo et al. 2019). The functional and taxonomic diversity of reef fish assemblages varies in habitats dominated by different coral species and with varying structural complexity (Komyakova et al. 2018), since corals provide microhabitats, shelter and food resources for coral reef fish species (Komyakova et al. 2013). In Caribbean reefs, differences in coral species can drive differences in reef fish species, in addition to other environmental variables (Arias-González et al. 2008, Rodríguez-Zaragoza and Arias-González 2008). Across the entire Indo-Pacific, an exceptionally similar pattern of coral and reef fish species richness in assemblages is observed, driven by coral area (Bellwood and Hughes 2001).

The distance from the biodiversity center was the environmental predictor that had higher relative importance for both total taxonomic and functional beta diversity in TEP (R^2 =0.89 and R^2 = 0.74, respectively). In our study, two biodiversity centers were considered: the Caribbean, for the Atlantic realm and the Indo-Australian Archipelago, for the Indo-Pacific realm. Both regions show different ecological and evolutionary history (Cowman & Bellwood 2013, Floeter et al. 2008). The Indo-Australian Archipelago has acted as a center of origin and was able to export reef fish species, mainly for the Indian and Pacific Oceans (Bellwood et al. 2012, Bellwood et al. 2015). The Caribbean represents only about 20% of the richness species found on the Indo-Pacific realm (Bellwood and Hughes 2001) but is still a biodiversity center in the Atlantic Ocean (Floeter et al. 2008). The distance from the center of biodiversity largely influences reef fish assemblage structure, from a taxonomic, functional and phylogenetic perspective (Bellwood and Hughes 2001, Bender et al. 2013, Leprieur et al. 2016, Bender et al. 2017).

At the marine realm scale, historical and evolutionary processes can explain recent patterns of reef fish assembly (Leprieur et al. 2016). The Quaternary period (~2.6 Ma to present) was characterized by fluctuations in global temperatures and sea-level shifts (Pellissier et al. 2014). Some stable coral reef areas may have developed a refugia role for reef organisms (Cowman and Bellwood 2013), promoting coral reef fish diversity (Pelissier et al. 2014). For instance, areas near to the Quaternary refugia have higher reef fish diversity, highlighting the importance of stable reef areas for the maintenance of species during the Quaternary (Pellissier et al. 2014). The Indo-Pacific realm, including the Indo-Australian Archipelago, Maldives, Madagascar and Red Sea areas, maintained stable and extensive coral reef refugia during sea level and temperature variations (Pellissier et al. 2014). This evidence is supported by hypotheses that consider these areas as centers of origin, overlap, survival and export of reef fish species (Bellwood et al. 2015). However, for the Atlantic realm, the distance from Quaternary refugia was not a variable with high relative importance for observed patterns of taxonomic and functional beta diversity ($R^2 = 0.26$ and $R^2 = 0.23$, respectively). During the cold Quaternary periods, only limited areas of the Caribbean were suitable for coral reefs, limiting the possible refugia for reef fish species (Pellissier et al. 2014). Beyond the Caribbean, the Indo-Australian Archipelago provides refuge from extinction in peripheral areas, due to its extensive shallow-water availability (Bellwood and Hughes 2001).

For total taxonomic beta diversity, isolation from the nearest reef areas had greater importance ($R^2 = 0.62$) in the Indo-Pacific realm. Studies have already shown the influence of this isolation measure on taxonomic and functional diversity for tropical reef fish in tropical environments (Kulbicki et al. 2013, Bender et al. 2017). The Indo Pacific realm is characterized by the connectivity between its biogeographic regions, which enables dispersal across the Indian and Pacific Oceans (Cowman and Bellwood 2013). Furthermore, isolation leads to functional and taxonomic nestedness of reef fish assemblages (Bender et al. 2017). Despite being an important variable in explaining current patterns of reef fish richness at different spatial scales (Bellwood and Hughes 2001, Bellwood et al. 2005, Parravicini et al. 2013), current reef area was not a good predictor for taxonomic and functional beta diversity in reef fish assemblages at the marine realm scale.

Our results demonstrate that functional beta diversity is positively correlated with taxonomic beta diversity, across marine realms and biogeographic regions. That is, greater variations in taxonomic composition between pairs of assemblages are followed by greater changes in functional composition. Studies that correlate both functional and taxonomic beta diversity are few in marine ecosystems. Atlantic reef fish communities have higher functional group richness in more speciose assemblages (Halpern and Floeter 2008). However, there is an uneven species distribution within functional groups. There are many vulnerable functional groups, where the functions are represented by a single species, showing high functional vulnerability (Halpern and Floeter 2008, Mouillot et al. 2014). Moreover, even though coral reefs are highly diversified and characterized by over-redundancy, high vulnerability and the lack of functions at the local scale could still compromise reef dynamics (Mouillot et al. 2014).

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6. Tables:

Table 1. Stress values obtained from two-dimensional NMDS ordinations of taxonomic and functional beta-diversity of reef fish faunas.

Realms	**Stress values**			
	T$ß_{sor}$	**T$ß_{sim}$**	**F$ß_{sor}$**	**F$ß_{sim}$**
Atlantic	0.045	0.063	0.035	0.108
Tropical Eastern Pacific	0.049	0.077	0.00005	0
Indo-Pacific	0.105	0.211	0.037	0.233
Indo-Pacific biogeographic regions	**Stress values**			
	T$ß_{sor}$	**T$ß_{sim}$**	**F$ß_{sor}$**	**F$ß_{sim}$**
Central Indo-Pacific	0.086	0.212	0.089	0.157
Central Pacific	0.063	0.156	0.040	0.195
Western Indian	0.074	0.166	0.076	0.172

Legend: T$ß_{sor}$: total taxonomic beta-diversity (Sorensen index); T$ß_{sim}$: taxonomic turnover; F$ß_{sor}$: total functional beta-diversity (Sorensen index), and F$ß_{sim}$: functional turnover.

Table 2. The association between environmental predictors with the NMDS ordination scores for total taxonomic (Tß$_{sor}$) and total functional beta diversity (Fß$_{sor}$) of reef fish assemblages in the Atlantic, the Tropical Eastern Pacific and the Indo-Pacific realms. Association is represented by regression coefficients from “envfit” analysis.

	Atlantic realm – Tß$_{sor}$			**Atlantic realm – Fß$_{sor}$**		
Predictors	**NMDS1**	**NMDS2**	**R^2**	**NMDS1**	**NMDS2**	**R^2**
Reef area	-0.62	0.78	0.31***	-0.58	-0.82	0.25**
Refugia	0.74	-0.67	0.26**	0.73	0.69	0.23*
Chlorophyll-a	0.47	0.89	0.06	-0.10	1.00	0.17*
Isolation	0.48	-0.88	0.43***	0.77	0.64	0.38**
SST	-0.96	0.27	0.44***	-0.72	-0.70	0.40***
Coral richness	-0.76	0.66	0.67***	-0.58	-0.82	0.60***

	TEP realm – Tß$_{sor}$			**TEP realm – Fß$_{sor}$**		
Predictors	**NMDS1**	**NMDS2**	**R^2**	**NMDS1**	**NMDS2**	**R^2**
Reef area	-0.61	-0.79	0.24	-0.52	0.86	0.25**
Refugia	-0.53	-0.85	0.07	-0.36	0.93	0.02
Chlorophyll-a	0.86	0.52	0.10	0.69	-0.72	0.16
Distance BC	0.89	-0.47	0.89***	0.99	0.13	0.74***
Isolation	0.04	-1.00	0.49**	0.19	0.98	0.44**
SST	-0.35	0.94	0.53***	-0.70	-0.71	0.23
Coral richness	-0.57	0.83	0.25	-0.86	-0.51	0.10

	Indo-Pacific realm – Tß$_{sor}$			**Indo-Pacific realm – FB$_{sor}$**		
Predictors	**NMDS1**	**NMDS2**	**R^2**	**NMDS1**	**NMDS2**	**R^2**
Reef area	0.82	0.57	0.03*	0.96	0.27	0.01
Refugia	-0.87	-0.49	0.62***	-0.64	0.77	0.52***
Chlorophyll-a	0.35	-0.94	0.16***	0.82	-0.57	0.00
Isolation	-0.96	-0.28	0.62***	-0.91	0.42	0.40***
SST	0.90	0.45	0.37***	0.99	-0.11	0.13***
Coral richness	0.89	0.46	0.38***	0.98	0.18	0.07***

Predictors: Reef area: current reef area; Refugia: distance from the Quaternary Refugia; Chlo: mean chlorophyll-a; Distance BC: distance from Biodiversity center; SST: mean sea surface temperature; Isolation: isolation from the nearest reef areas and Coral richness. *** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$.

7. Figures:

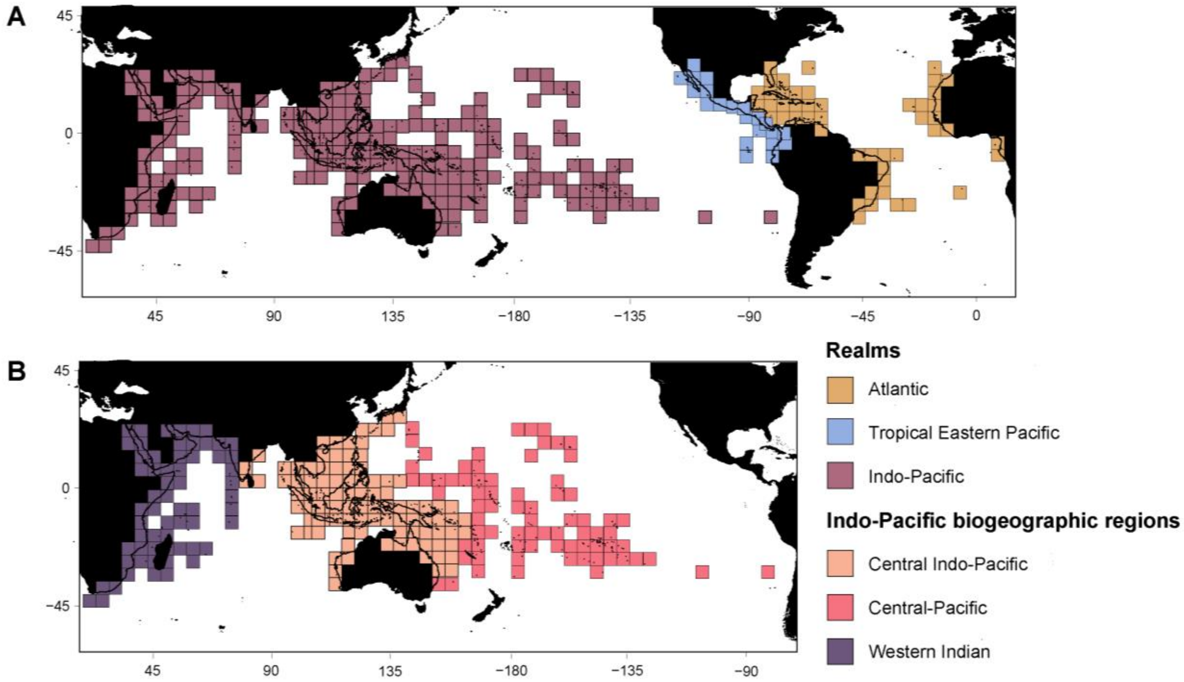

Figure 1. The global distribution of reef fish assemblages in (A) three marine realms and (B) three biogeographic regions within the Indo-Pacific realm. Based on marine realms and biogeographic regions from the study of Kulbicki et al. (2013).

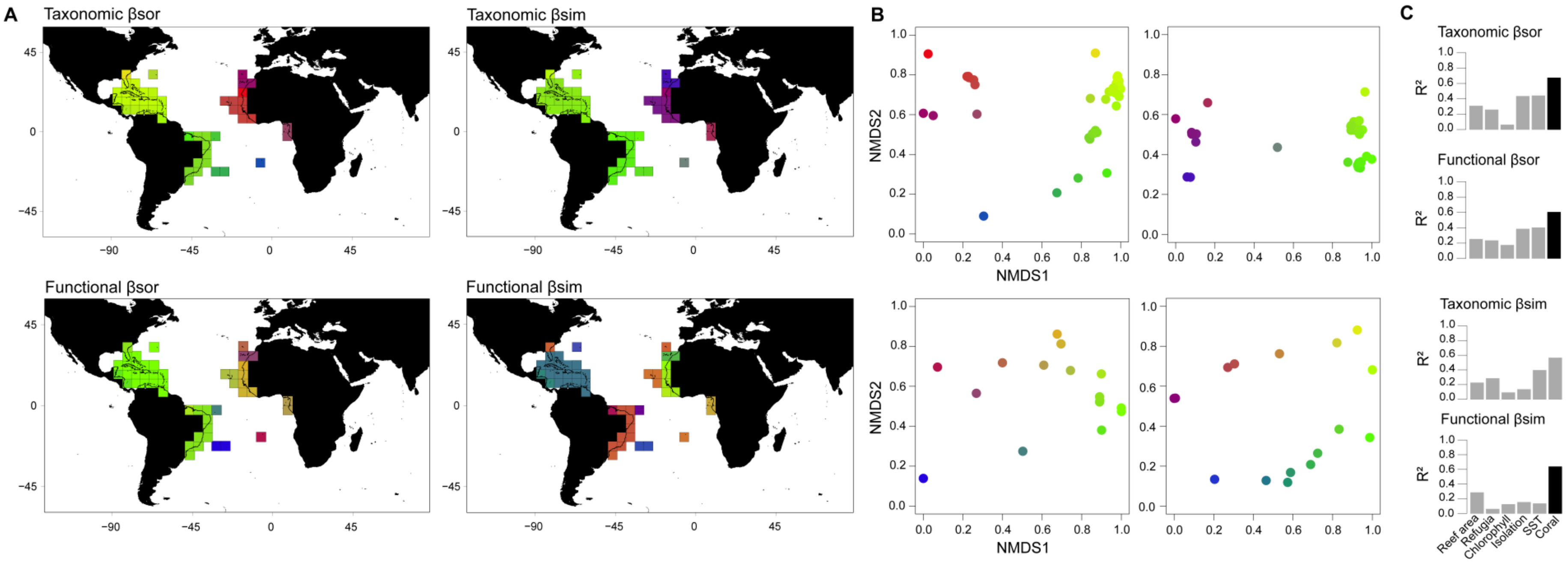

Figure 2. The Atlantic reef fish beta-diversity patterns inferred from non-metric multidimensional scaling (NMDS) ordination based on (A) the total taxonomic beta diversity (Taxonomic ß$_{sor}$) and total functional beta diversity (Functional ß$_{sor}$) as well as the taxonomic turnover component (Taxonomic ß$_{sim}$) and functional turnover component (Functional ß$_{sim}$). In (B) Each dot in the NMDS scatters plots represents a grid cell and colors are identical to those in the map. (C) The relative importance (R^2) of environmental predictors (Current reef area; Distance from Quaternary Refugia; mean Chlorophyll-a; Distance from the biodiversity center; Isolation from the nearest reef areas; Mean sea surface temperature and Coral richness) to taxonomic and functional beta diversity from the “envfit” analysis. Black bars denote environmental variables with relative importance $R^2 \geq 0.6$.

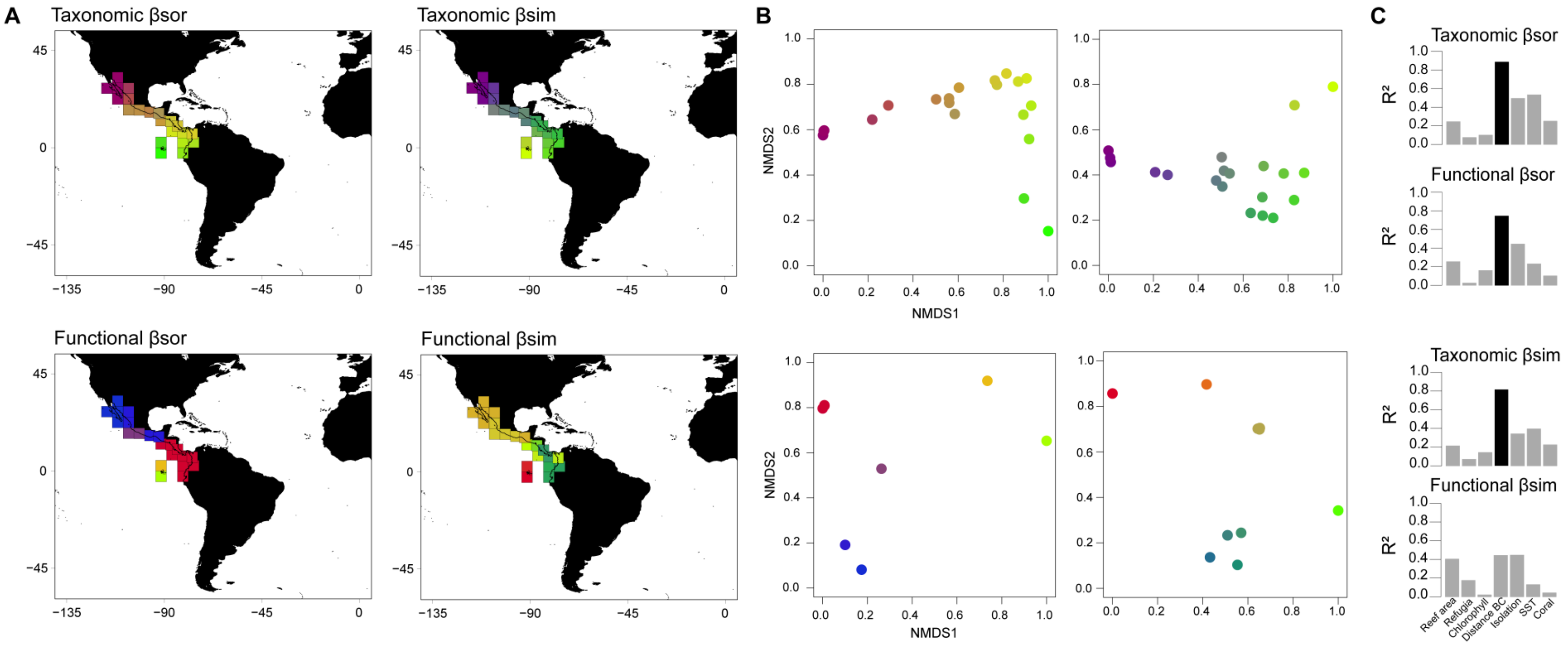

Figure 3. The Tropical Eastern Pacific reef fish beta-diversity patterns inferred from non-metric multidimensional scaling (NMDS) ordination based on (A) the total taxonomic beta diversity (Taxonomic $ß_{sor}$) and total functional beta diversity (Functional $ß_{sor}$) as well as the taxonomic turnover component (Taxonomic $ß_{sim}$) and functional turnover component (Functional $ß_{sim}$). In (B) Each dot in the NMDS scatters plots represents a grid cell and colors are identical to those in the map. (C) The relative importance (R^2) of environmental predictors (Current reef area; Distance from Quaternary Refugia; mean Chlorophyll-a; Distance from the biodiversity center; Isolation from the nearest reef areas; Mean sea surface temperature and Coral richness) to taxonomic and functional beta diversity from the "envfit" analysis. Black bars denote environmental variables with relative importance $R^2 \geq 0.6$.

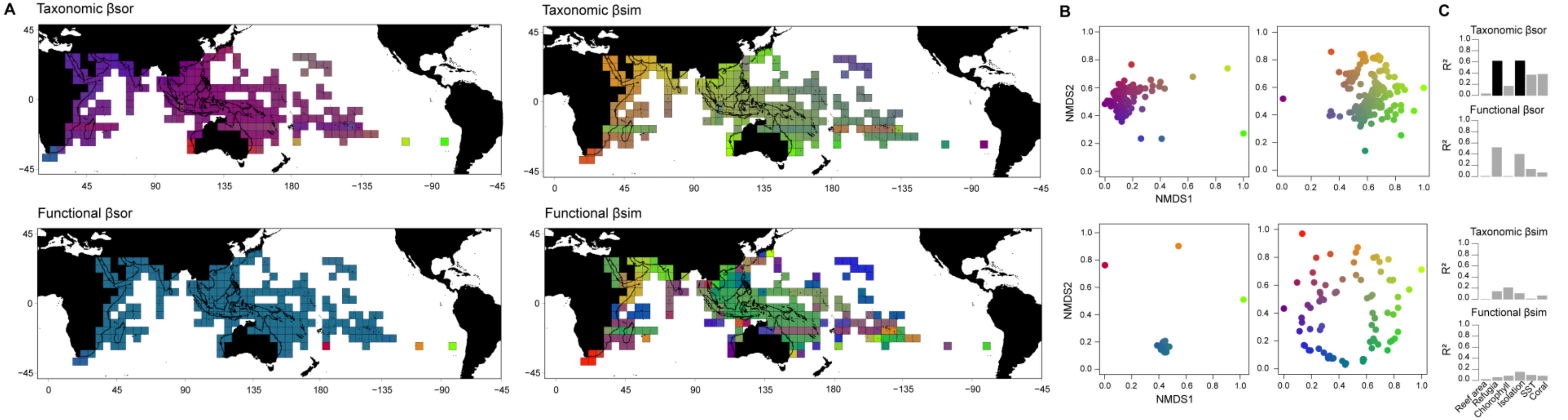

Figure 4. The Indo-Pacific reef fish beta-diversity patterns inferred from non-metric multidimensional scaling (NMDS) ordination based on (A) the total taxonomic beta diversity (Taxonomic ß$_{\mathrm{sor}}$) and total functional beta diversity (Functional ß$_{\mathrm{sor}}$) as well as the taxonomic turnover component (Taxonomic ß$_{\mathrm{sim}}$) and functional turnover component (Functional ß$_{\mathrm{sim}}$). In (B) Each dot in the NMDS scatters plots represents a grid cell and colours are identical to those in the map. (C) The relative importance (R^2) of environmental predictors (Current reef area; Distance from Quaternary Refugia; mean Chlorophyll-a; Isolation from the nearest reef areas; Mean sea surface temperature and Coral richness) to taxonomic and functional beta diversity from the “envfit” analysis. Black bars denote environmental variables with relative importance $R^2 \geq 0.6$.

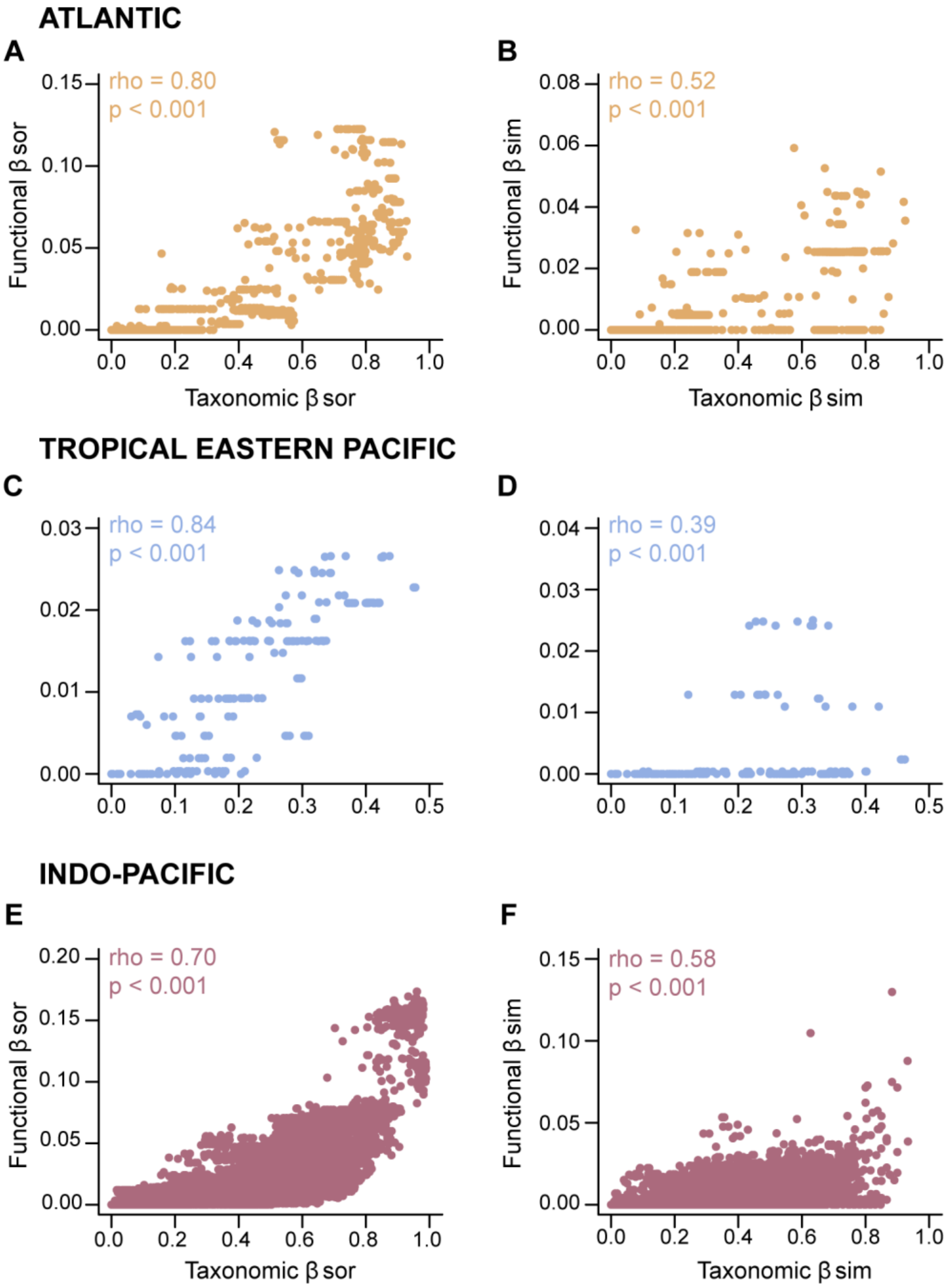

Figure 5. Spearman’s correlation coefficients between taxonomic and functional beta diversity, including total beta diversity (left hand side) and the turnover (right hand side) component of reef fish assemblages in the Atlantic (A, B), the Tropical Eastern Pacific (C, D) and the Indo-Pacific realms (E, F).

8. Supplementary material:

Table S1. Geographic and environmental predictors utilized in each marine realm and biogeographic regions.

Realms	**Variables**
Atlantic	Reef area; Refugia; Chlo; Isolation; SST and Coral richness
Tropical Eastern Pacific	Reef area; Refugia; Chlo; Distance BC; Isolation; SST and Coral richness
Indo-Pacific	Reef area; Refugia; Chlo; Isolation; SST and Coral richness
Indo-Pacific biogeographic regions	
Central Indo-Pacific	Reef area; Refugia; Chlo; Distance BC; Isolation and Coral richness
Central Pacific	Reef area; Refugia; Chlo; Distance BC; SST and Coral richness
Western Indian	Reef area; Refugia; Chlo; Distance BC; Isolation and Coral richness

Legend: Reef area: current reef area; Refugia: distance from the Quaternary Refugia; Chlo: mean Chlorophyll-a; Distance BC: distance from the biodiversity center; SST: mean sea surface temperature; Isolation: isolation from the nearest reef areas and Coral richness.

Table S2. The environmental predictors considered in this study for the Central Indo-Pacific, the Central Pacific and the Western Indian biogeographic regions and their association with the NMDS ordination scores for taxonomic (Tß$_{sor}$) and functional beta diversity (Fß$_{sor}$) of reef fish assemblages. Association is represented by regression coefficients from "envfit" analysis.

	Central Indo-Pacific – Tß$_{sor}$			**Central Indo-Pacific – Fß$_{sor}$**		
Predictors	**NMDS1**	**NMDS2**	**R^2**	**NMDS1**	**NMDS2**	**R^2**
Reef area	0.25	-0.97	0.02	-0.13	0.99	0.03
Refugia	-0.46	-0.89	0.46***	-0.34	-0.94	0.39***
Chlorophyll-a	0.01	1.00	0.11*	0.78	-0.63	0.01
Distance BC	-0.07	-1.00	0.14**	-0.97	-0.26	0.32***
Isolation	-0.89	-0.46	0.55***	-0.10	-1.00	0.38***
Coral richness	0.69	0.72	0.11**	0.42	0.91	0.39***

	Central Pacific – Tß$_{sor}$			**Central Pacific – Fß$_{sor}$**		
Predictors	**NMDS1**	**NMDS2**	**R^2**	**NMDS1**	**NMDS2**	**R^2**
Reef area	0.58	0.82	0.07	0.21	-0.98	0.07
Refugia	-1.00	-0.04	0.69***	-0.92	0.39	0.85***
Chlorophyll-a	0.20	-0.98	0.03	-0.02	-1.00	0.07
Distance BC	-0.96	-0.27	0.10*	-0.08	1.00	0.10*
Mean SST	0.80	0.60	0.56***	0.59	0.81	0.54***
Coral richness	0.97	-0.26	0.40***	0.87	-0.50	0.25***

	Western Indian – Tß$_{sor}$			**Western Indian – FB$_{sor}$**		
Predictors	**NMDS1**	**NMDS2**	**R^2**	**NMDS1**	**NMDS2**	**R^2**
Reef area	0.91	-0.43	0.12*	-0.19	0.98	0.14**
Refugia	-0.99	-0.17	0.75***	-0.74	-0.68	0.36***
Chlorophyll-a	-0.05	1.00	0.33**	-0.06	-1.00	0.07
Distance BC	-0.90	-0.44	0.16**	-1.00	-0.08	0.33***
Isolation	-0.74	-0.68	0.41***	-0.98	-0.21	0.19***
Coral richness	0.46	-0.89	0.68***	0.21	0.98	0.42***

Predictors: Reef area: current reef area; Refugia: distance from the Quaternary Refugia; Chlorophyll-a: mean chlorophyll-a; Distance BC: distance from biodiversity center; SST: mean sea surface temperature; Isolation: isolation from the nearest reef areas and Coral richness. *** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$.

Table S3. The association between environmental predictors with the NMDS ordination scores for taxonomic (Tß$_{sim}$) and functional turnover (Fß$_{sim}$) of reef fish assemblages in the Atlantic, the Tropical Eastern Pacific and the Indo-Pacific realms. Association is represented by regression coefficients from "envfit" analysis.

	Atlantic realm – Tß$_{sim}$			**Atlantic realm – Fß$_{sim}$**		
Predictors	**NMDS1**	**NMDS2**	**R^2**	**NMDS1**	**NMDS2**	**R^2**
Reef area	-0.29	0.96	0.23**	0.99	-0.12	0.29***
Refugia	0.23	-0.97	0.28***	-0.99	-0.14	0.06
Chlorophyll-a	0.26	0.97	0.09	-0.24	0.97	0.12*
Isolation	0.86	0.50	0.13*	-0.97	0.24	0.15*
SST	-0.40	0.92	0.40***	0.73	-0.69	0.13*
Coral richness	-0.35	0.94	0.56***	0.97	-0.24	0.64***

	TEP realm – Tß$_{sim}$			**TEP realm – Fß$_{sim}$**		
Predictors	**NMDS1**	**NMDS2**	**R^2**	**NMDS1**	**NMDS2**	**R^2**
Reef area	-0.72	0.69	0.21	0.07	-1.00	0.40**
Refugia	-0.96	-0.27	0.07	0.14	-0.99	0.18
Chlorophyll-a	0.46	-0.89	0.14	-0.15	0.99	0.02
Distance BC	0.83	0.56	0.82***	-0.81	0.58	0.44**
Isolation	-0.03	1.00	0.34*	-0.51	-0.86	0.45**
SST	-0.35	-0.94	0.39*	0.59	0.81	0.13
Coral richness	-0.53	-0.85	0.23	0.96	-0.27	0.04

	Indo-Pacific realm – Tß$_{sim}$			**Indo-Pacific realm – FB$_{sim}$**		
Predictors	**NMDS1**	**NMDS2**	**R^2**	**NMDS1**	**NMDS2**	**R^2**
Reef area	0.55	0.83	0.00	0.84	0.54	0.02
Refugia	-0.01	-1.00	0.14***	-0.78	-0.63	0.06***
Chlorophyll-a	-0.83	0.56	0.21***	-0.31	0.95	0.08***
Isolation	0.34	-0.94	0.11***	-0.17	-0.99	0.15***
SST	-0.45	0.89	0.01	0.58	0.81	0.10***
Coral richness	-0.01	1.00	0.06***	0.61	0.79	0.08***

Predictors: Reef area: current reef area; Refugia: distance from the Quaternary Refugia; Chlorophyll-a: mean chlorophyll-a; Distance BC: distance from biodiversity center; SST: mean sea surface temperature; Isolation: isolation from the nearest reef areas and Coral richness. *** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$.

Table S4. The environmental predictors considered in this study for the Central Indo-Pacific, the Central Pacific and the Western Indian biogeographic regions and their association with the NMDS ordination scores for taxonomic (Tß$_{sim}$) and functional turnover (Fß$_{sim}$) of reef fish assemblages. Association is represented by regression coefficients from "envfit" analysis.

	Central Indo-Pacific – Tß$_{sim}$			**Central Indo-Pacific – Fß$_{sim}$**		
Predictors	**NMDS1**	**NMDS2**	**R^2**	**NMDS1**	**NMDS2**	**R^2**
Reef area	-0.73	0.68	0.04	0.98	-0.18	0.02
Refugia	-0.82	-0.57	0.47***	-0.48	-0.88	0.08*
Chlorophyll-a	0.51	-0.86	0.05	-0.91	0.41	0.02
Distance BC	-0.61	0.79	0.46***	0.86	0.52	0.23***
Isolation	-0.85	-0.53	0.18**	-0.99	-0.17	0.13**
Coral richness	1.00	0.10	0.08*	0.88	0.47	0.01

	Central Pacific – Tß$_{sim}$			**Central Pacific – Fß$_{sim}$**		
Predictors	**NMDS1**	**NMDS2**	**R^2**	**NMDS1**	**NMDS2**	**R^2**
Reef area	0.42	0.91	0.03	-0.67	0.74	0.06
Refugia	0.63	-0.78	0.30**	-0.87	-0.49	0.03
Chlorophyll-a	-0.03	-1.00	0.10*	-0.43	-0.90	0.24***
Distance BC	-0.43	0.90	0.35***	0.31	0.95	0.13**
Mean SST	-0.28	0.96	0.15**	0.96	0.28	0.14**
Coral richness	-0.74	-0.67	0.05	0.16	-0.99	0.00

	Western Indian – Tß$_{sim}$			**Western Indian – FB$_{sim}$**		
Predictors	**NMDS1**	**NMDS2**	**R^2**	**NMDS1**	**NMDS2**	**R^2**
Reef area	0.53	0.85	0.22**	0.56	-0.83	0.18**
Refugia	-0.86	-0.51	0.44***	0.17	-0.99	0.02
Chlorophyll-a	0.45	-0.90	0.30***	-0.45	0.89	0.12*
Distance BC	-0.97	0.26	0.03	0.97	-0.26	0.25***
Isolation	-0.96	0.27	0.26***	-0.07	-1.00	0.18**
Coral richness	0.16	0.99	0.75***	0.60	-0.80	0.27**

Predictors: Reef area: current reef area; Refugia: distance from the Quaternary Refugia; Chlorophyll-a: mean chlorophyll-a; Distance BC: distance from biodiversity center; SST: mean sea surface temperature; Isolation: isolation from the nearest reef areas and Coral richness. *** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$.

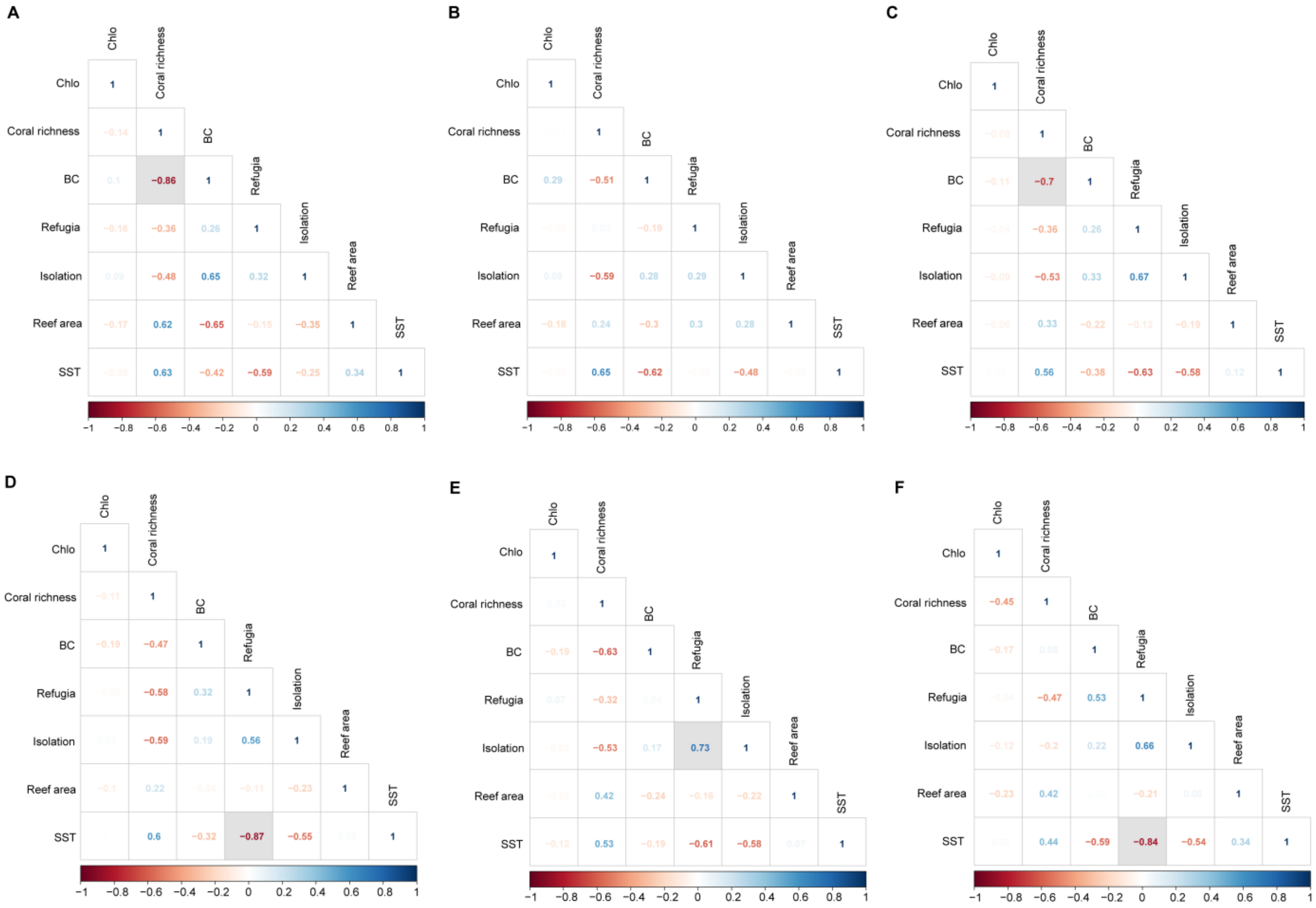

Figure S1. Correlation matrices for the set of environmental and geographic predictors for marine realms (A) the Atlantic, (B) the Tropical Eastern Pacific, (C) the Indo-Pacific and biogeographic regions of the Indo-Pacific realm (D) the Central Indo-Pacific, (E) the Central Pacific and (F) the Western Indian. Filled grey square indicates environmental predictors with correlation ≥ 0.7. When two predictors were correlated, one was excluded from the analysis. Predictors: Chlo: mean chlorophylla-a; Coral richness; BC: distance from biodiversity center; Refugia: distance from Quaternary refugia; Isolation: isolation from the nearest reef areas; Reef area: current reef area; and SST: mean sea surface temperature.

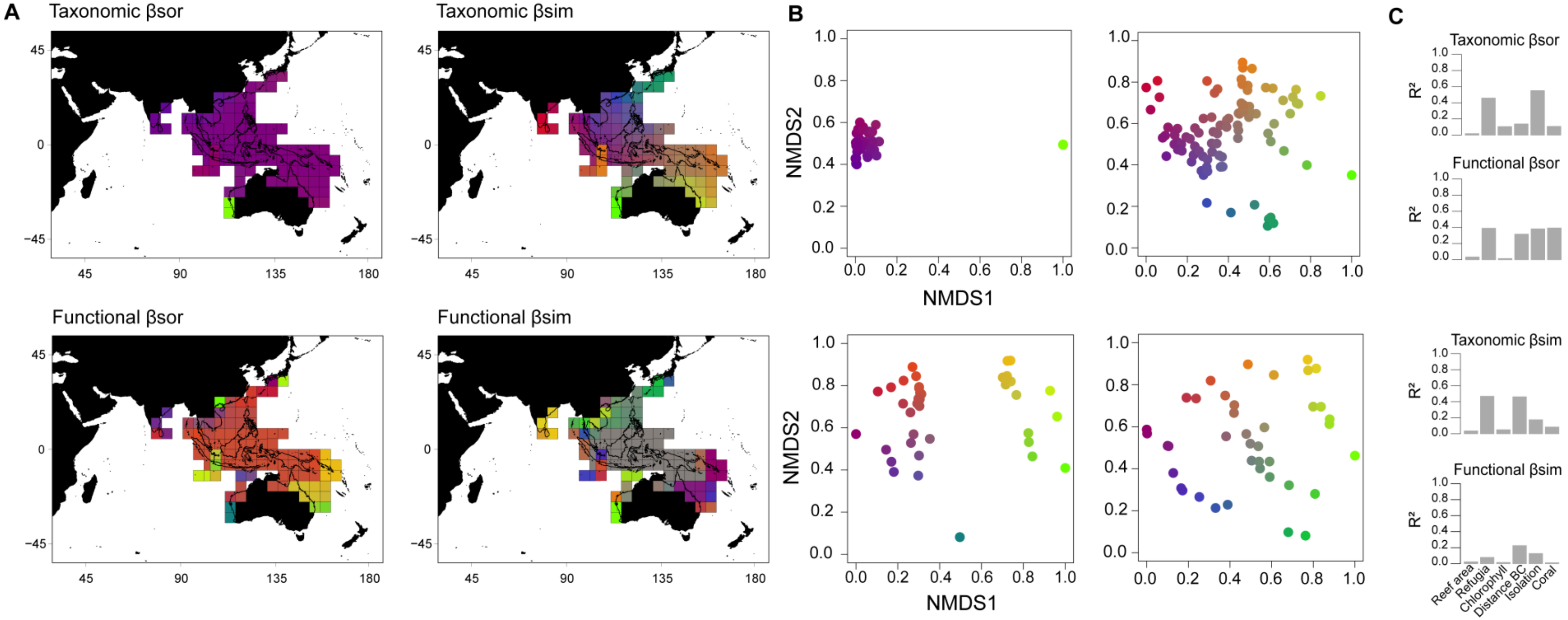

Figure S2. The Central Indo-Pacific reef fish beta-diversity patterns inferred from non-metric multidimensional scaling (NMDS) ordination based on (A) the total taxonomic beta diversity (Taxonomic $ß_{sor}$) and total functional beta diversity (Functional $ß_{sor}$) as well as the taxonomic turnover component (Taxonomic $ß_{sim}$) and functional turnover component (Functional $ß_{sim}$). In (B) Each dot in the NMDS scatters plots represents a grid cell and colors are identical to those in the map. (C) The relative importance (R^2) of environmental predictors (Current reef area; Distance from Quaternary Refugia; mean Chlorophyll-a; Distance from the biodiversity center; Isolation from the nearest reef areas and Coral richness) to taxonomic and functional beta diversity from the "envfit" analysis. Black bars denote environmental variables with relative importance $R^2 \geq 0.6$.

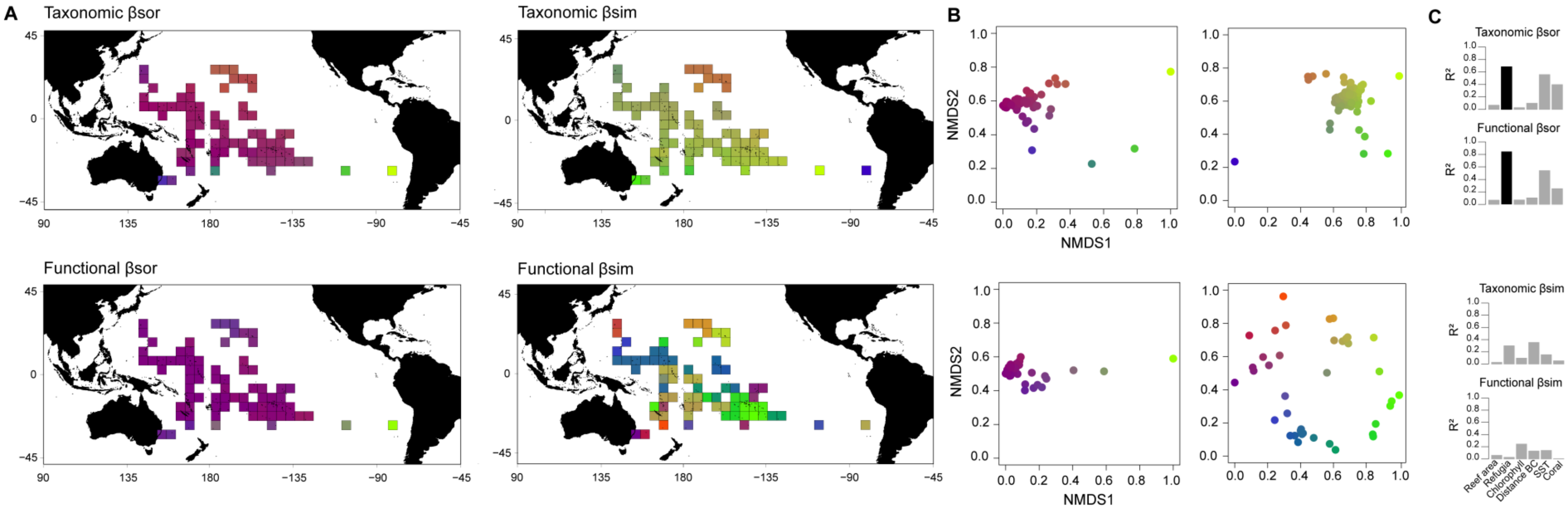

Figure S3. The Central Pacific reef fish beta-diversity patterns inferred from non-metric multidimensional scaling (NMDS) ordination based on (A) the total taxonomic beta diversity (Taxonomic ß$_{sor}$) and total functional beta diversity (Functional ß$_{sor}$) as well as the taxonomic turnover component (Taxonomic ß$_{sim}$) and functional turnover component (Functional ß$_{sim}$). In (B) Each dot in the NMDS scatters plots represents a grid cell and colors are identical to those in the map. (C) The relative importance (R^2) of environmental predictors (Current reef area; Distance from Quaternary Refugia; mean Chlorophyll-a; Distance from the biodiversity center; Mean sea surface temperature and Coral richness) to taxonomic and functional beta diversity from the "envfit" analysis. Black bars denote environmental variables with relative importance $R^2 \geq 0.6$.

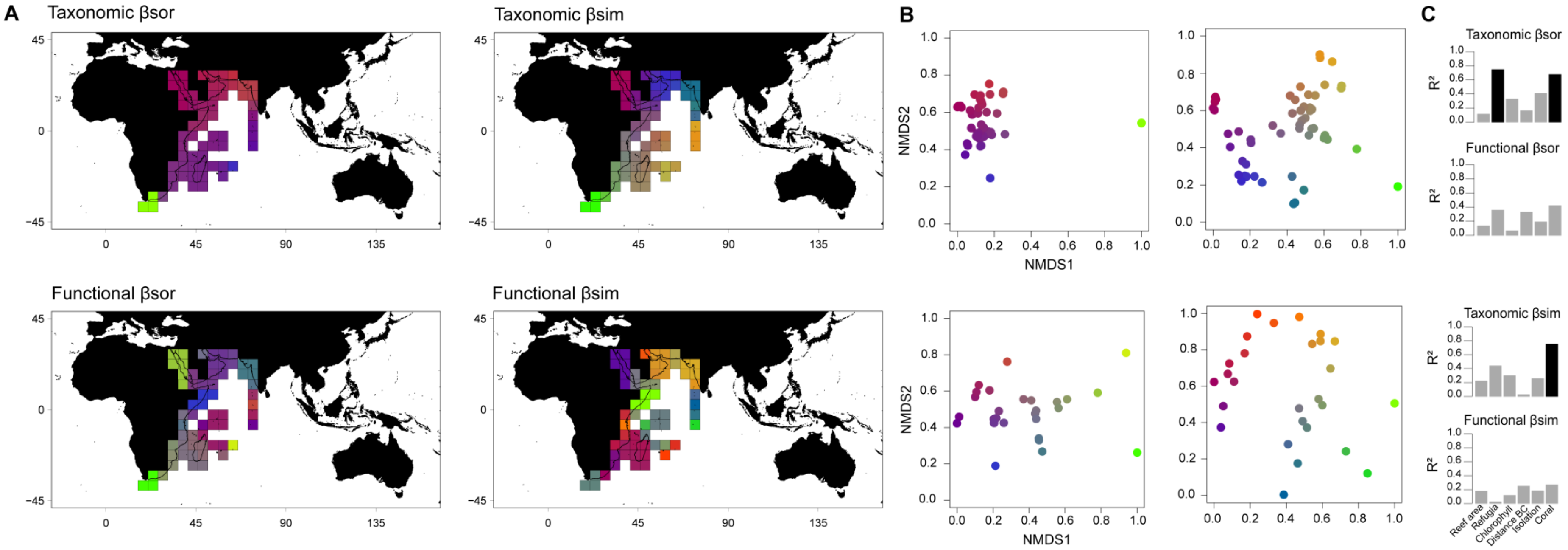

Figure S4. Figure S2. The Western Indian reef fish beta-diversity patterns inferred from non-metric multidimensional scaling (NMDS) ordination based on (A) the total taxonomic beta diversity (Taxonomic ß$_{\mathrm{sor}}$) and total functional beta diversity (Functional ß$_{\mathrm{sor}}$) as well as the taxonomic turnover component (Taxonomic ß$_{\mathrm{sim}}$) and functional turnover component (Functional ß$_{\mathrm{sim}}$). In (B) Each dot in the NMDS scatters plots represents a grid cell and colors are identical to those in the map. (C) The relative importance (R^2) of environmental predictors (Current reef area; Distance from Quaternary Refugia; mean Chlorophyll-a; Distance from the biodiversity center; Isolation from the nearest reef areas and Coral richness) to taxonomic and functional beta diversity from the “envfit” analysis. Black bars denote environmental variables with $R^2 \geq 0.6$.

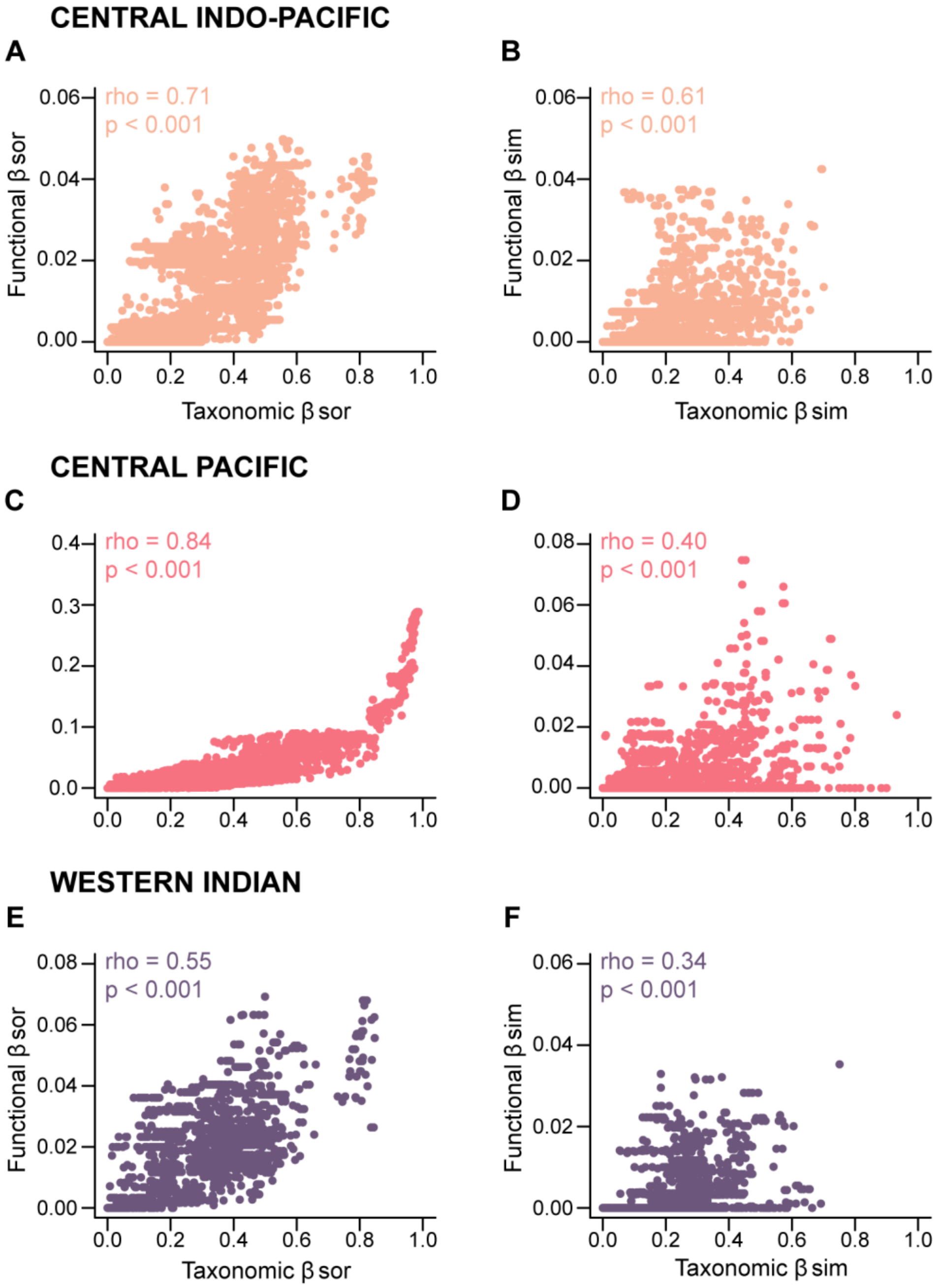

Figure S5. Spearman’s correlation coefficients between taxonomic and functional beta diversity, including total beta diversity (left hand side) and the turnover component (right hand side) of reef fish assemblages in three Indo-Pacific biogeographic regions: the Central Indo-Pacific (A, B), the Central Pacific (C, D) and the Western Indian (E, F).